

Brief report

Colour morph does not predict brood size in the Booted Eagle

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Received 22 October 2015, accepted 19 February 2016

Mechanisms regulating colour polymorphism remain largely unknown and detailed investigation is required to explore the biological consequences on population dynamics. This paper presents the first study of the possible connection between colour polymorphism and productivity in a Booted Eagle (*Aquila pennata*) population breeding in south-eastern Spain. To that end we used 19 years of data of non-marked individuals. A total of 738 pale (91.6%) and 68 dark (8.4%) adult Booted Eagles were observed in our study area, including 57 territories. Our results suggest that colour morph of both sexes remained stable in the population over the study period. Although we found a higher number of offspring produced by parents exhibiting the dark morph than those of the pale morph, statistical differences were not significant. Hence, our models showed that colour polymorphism was not a good predictor of Booted Eagles' productivity, although further research by capture-recapture analysis would be needed to explore the influence of colour variation on fitness components at individual level and its consequences at population level of long-lived species.



1. Introduction

Polymorphism in colour is a widespread phenomenon in many animal taxa, and it is defined as the coexistence of two or more distinct and genetically determined colour morphs in one interbreeding

population (Huxley 1955). Melanin-based colour variation within and between bird species normally has a strong genetic component (Hrubant 1955, Lank *et al.* 1995, Roulin *et al.* 1998, Krüger *et al.* 2001, Roulin & Dijkstra 2003), and such intraspecific colour variation is independent of sex,

age and season (Butcher & Rohwer 1989), although it can occur in different frequency due to a geographical range (Burri *et al.* 2016). Despite the mechanisms responsible for the evolution and maintenance of colour polymorphisms in wild populations have been subject of intensive research (Sinervo & Lively 1996, Roulin 2004a, Gray & McKinnon 2007), this phenomenon still remains poorly understood (Galeotti *et al.* 2003, Roulin 2004a, Boerner & Krüger 2009).

One of the bird groups where colour polymorphism is most common are raptors (Chakarov *et al.* 2011). However, causal mechanisms regulating colour polymorphism remain largely unknown and more research is required to describe such patterns and the possible mechanisms that influence their occurrence (Johnson & Burnham 2013). In taxa exhibiting polymorphism, several hypotheses have been suggested about its biological consequences, including offspring production (Krüger *et al.* 2001, Johnson & Burnham 2013), predation risk (Roulin & Wink 2004), dispersal (Roulin 2013, Chakarov *et al.* 2013), differences in hatching date (Chakarov *et al.* 2011), bacterial infections (Saggese *et al.* 2008), ecto- and endoparasite burden (Galeotti & Sacchi 2003, Roulin 2004b, Chakarov *et al.* 2008), moult patterns (Brommer *et al.* 2003), behaviour (Korzan & Fernald 2007, Boerner & Krüger 2009, Bortolotti *et al.* 2011, Da Silva *et al.* 2013) and sexual selection (Roulin 2016). Nevertheless, to date, no information exist on the factors that may influence colour variation or its adaptive function in Booted Eagles *Aquila pennata*, a species for which the genetic basis of polymorphism still remains unknown (Galván *et al.* 2010).

The Booted Eagle is a long-lived trans-Saharan migrant which arrives in Europe in late March and leaves in late September (Cramp & Simmons 1980, Mellone *et al.* 2013, 2015). Although some individuals winter in the Mediterranean basin (Martínez & Sánchez-Zapata 1999), the majority of the population migrates to the Sahel region and tropical Africa (Cramp & Simmons 1980, Mellone *et al.* 2013). Booted Eagles use elaborated aerial displays to establish monogamous pair bond (Cramp & Simmons 1980), showing a high territory fidelity in the study area (Jiménez-Franco *et al.* 2013). In the breeding area, approximately one month after arrival (late April), females lay one to

two eggs, rarely three, and breed normally 1–2 young per nest (Cramp & Simmons 1980). Booted Eagles exhibit one of two distinct colour morphs, pale or dark, which remain during their lifetime with some geographic variation (Cramp & Simmons 1980, Forsman 1999). Some authors have suggested that the ratio between the two colour morphs varies geographically across Europe with a higher percentage of the pale morph in the West (e.g. 80% in Spain, 70% in France and Austria) and a lower percentage in the East (e.g. 60% in Greece and Middle East, 50% in Caucasus, 20–30% in Russia, Ukraine and Turkmenistan; Glutz von Blotzheim *et al.* 1971, Cramp & Simmons 1980, Ferguson-Lees & Christie 2001, Karyakin 2007). In this paper we explore the link between productivity and a highly heritable phenotypic trait, plumage coloration, in a Booted Eagles population in south-eastern Spain.

2. Material and methods

This study was conducted in a semi-arid Mediterranean mountainous area located in the Special Protection Area for Birds “Sierras de Burete, Lavia y Cambrón” (code ES0000267) located in the centre of Murcia province, south-eastern Spain (coordinates: 38°00'N, 1°45'W). The study area covers about 10,000 ha, with elevations ranging from 550 to 1,234 m above sea-level. The climate is Mediterranean with a mean annual rainfall of c. 400 mm concentrated mostly during the spring and autumn. The landscape is characterized by mountain slopes covered by Aleppo pine forests (*Pinus halepensis*) interspersed with traditional agricultural ecosystems (cereals, vineyards, olive and almond groves). For more details of the study area, see Jiménez-Franco *et al.* (2014).

Between 1995 and 2013, an intensive monitoring of 57 territories was carried out during the breeding season. Territory occupation was assessed each year from late March to early May. Occupancy was determined when signs of territorial or mating behaviour were observed, including courtship and territorial flights and responses (e.g., elicited vocalizations, approaches), copulations, nest material transfers, the presence of at least one freshly refurbished nest or direct evidence of reproduction (details in Martínez *et al.* 2006a,b). We

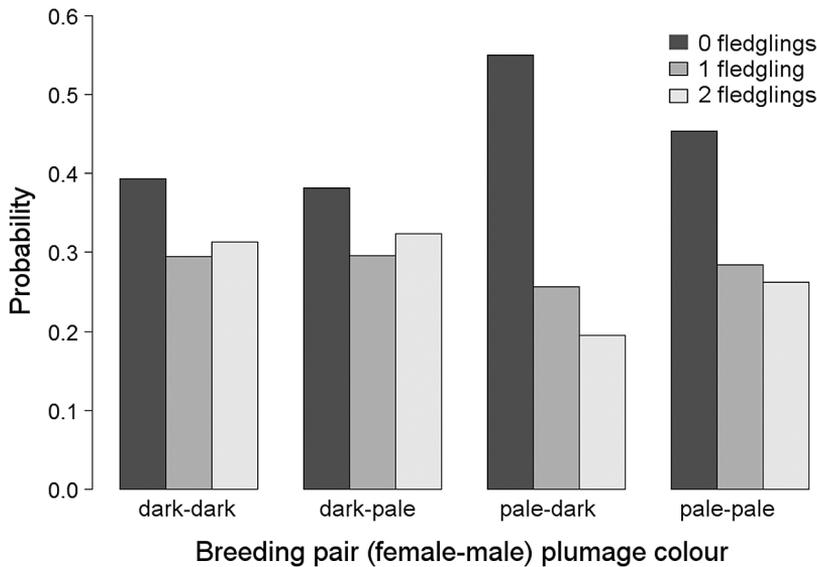


Fig. 1. Brood size probabilities fitted according to plumage colour of Booted Eagle pairs in south eastern Spain. Results are based on the mixed-effects ordinal regression model including an interaction term.

identified the plumage colouration in both pair members by direct observation (Galeotti & Sacchi 2003, Roulin *et al.* 2003, Brommer *et al.* 2005). Morph scoring followed the recognition scheme of Cramp & Simmons (1980), Del Hoyo *et al.* (1994) and Forsman (1999), where two morphs are recognized (dark and pale); with melanic individuals having a greater amount of eumelanic feathers. The sex of each individual was easily recognizable from its size and breeding behaviour (Jiménez-Franco *et al.* 2013). When a territory was occupied, at least three visits were made to record productivity (i.e., number of fledglings per monitored pair; Martínez *et al.* 2006a), considering those which survived to about 45 days old (Steenhof 1987).

Differences in the productivity in relation to plumage colour were tested using mixed-effects ordinal regression models. Following Otterbeck *et al.* (2015), we modelled productivity as an ordinal response variable (number of offspring: 0, 1, 2). We tested four different models using “male colour”, “female colour”, and their interaction were used as explanatory factors. To control for non-independence of breeding data, we included territory and year as random factors (affecting the intercept). Analyses were performed using the *clmm* function implemented in the *ordinal* package

(Christensen 2015) for R-software version 3.2.2 (R Core Team 2015), which does maximum likelihood estimation using Laplace approximation of the likelihood. The level of significance for statistical analyses was set at $\alpha = 0.05$.

3. Results

The pale morph was widely predominant (91.6%) over the study period, with only 68 of 806 individuals (8.4%) exhibiting the dark morph. Most of dark morph individuals were females (62 of 68; i.e., 91.2%).

In Fig. 1 we showed brood size probabilities fitted according to plumage colour of Booted Eagles in our study area (female–male; dark–dark, dark–pale, pale–dark and pale–pale). However, the mixed-effects ordinal regression models showed no significant effects of colour morph on breeding productivity (Table 1).

4. Discussion

The ratio between pale and dark morphs in our study area was very similar to other Booted Eagles populations in the Western Palearctic region,

Table 1. Summary of mixed-effects ordinal regression models on the number of fledglings (R) in 403 breeding events recorded in 57 territories of Booted Eagles in south-eastern Spain. DF: dark female; DM: dark male; t_i : territory effects; y_i : year effects. Columns "Territory" and "Year" report the fitted random effect standard deviations of these factors.

Model	Coefficient	SE	z	P	Territory	Year
$R = \beta_1 \text{DF} + \beta_2 \text{DM} + t_i + y_i$	$\beta_1 = 0.305$	0.298	1.024	0.306	0.739	0.421
	$\beta_2 = -0.197$	0.895	-0.220	0.826	–	–
$R = \beta_1 \text{DF} + \beta_2 \text{DM} + \beta_3 \text{DF} \times \text{DM} + t_i + y_i$	$\beta_1 = 0.297$	0.301	0.986	0.324	0.739	0.421
	$\beta_2 = -0.389$	1.365	-0.285	0.776	–	–
	$\beta_3 = 0.339$	1.796	0.189	0.850	–	–

where the pale morph is largely dominant (Ferguson-Lees & Christie 2001). A recent research has revealed that dark morph nestlings of Booted Eagles exhibit lower levels of glutathione, a key intracellular antioxidant that inhibits the synthesis of eumelanin, than those of lighter morphs (Galván *et al.* 2010). These authors also found that dark female eaglets had higher levels of antioxidants other than glutathione and were in better body condition than light female eaglets. This result suggests an adaptive response of dark nestlings to compensate for reduced glutathione levels. According to these authors, dark individuals may pay a fitness cost (lower fecundity and survival as compared to pale eagles). Thus, it would be expected that pale Booted Eagles had higher productivity than dark individuals. However, our results showed similar values of productivity between different morph combinations in the breeding pairs (Fig. 1, Table 1).

Previous studies have shown that plumage morph in polychromatic species is one important predictor of productivity (Krüger *et al.* 2001, Johnson & Burnham 2013, Gangoso *et al.* 2015) and lifetime reproductive success (Krüger 2002, Brommer *et al.* 2005), along with others factors such as competition, weather, and territory quality (Krüger 2002). Our results are not consistent with these works since our models do not show significant relationship between plumage colouration and offspring production (Table 1). However, our results should be taken with caution because we did not have marked individuals in our population and their individual lifetime reproductive success could not be assessed in the long term. In this line, Brommer *et al.* (2005) found that grey tawny owls do not produce more offspring per breeding attempt, but have a longer breeding lifespan than

brown individuals, and therefore manage to produce more fledglings and recruits during their lifetime. An additional hypothesis is needed to elucidate whether pale individuals have a longer breeding lifespan than dark individuals. In fact, lifespan is the main determinant of lifetime reproductive success in a variety of taxa (e.g., Clutton-Brock 1988). For this reason, pale Booted Eagles could not produce more offspring per breeding attempt, but could have a longer breeding lifespan than dark individuals, and therefore manage to produce more fledglings and recruits during their lifetime (Brommer *et al.* 2005). Previous studies in the same population of Booted Eagles suggested that nesting habitat quality, prey availability, predation, parasites and weather did not significantly influence productivity (Martínez *et al.* 2006a,b, Pagán *et al.* 2009, Jiménez-Franco *et al.* 2014, Bosch *et al.* 2015). These factors would be acting on natural selection in order to favour some phenotypic traits and the related effect on reproductive fitness (Price *et al.* 1984, Gibbs & Grant 1987, Galeotti *et al.* 2003, Roulin 2004a). Another possibility is that colour polymorphism is associated with offspring quality rather than offspring number (Roulin & Ducrest 2011). Considering the effect of habitat quality on productivity, high homogeneity in habitat quality, high prey availability and low precipitation, have scarce impact on individual fitness, and may explain the null effect of colour polymorphism on productivity (Karell *et al.* 2011). In fact, in the study area, reproductive output was related to individual quality instead of territory quality (Pagán *et al.* 2009, Jiménez-Franco *et al.* 2013, 2014). Therefore, future studies could include not only the effects of colour morph on Booted Eagle productivity, but also the interaction of colour polymorphism and habitat characteris-

tics (Dreiss *et al.* 2012). Moreover, other individual attributes such as body condition or experience of individuals should be also considered in order to understand the natural mechanism behind these results.

Finally, further studies, by capture-recapture analysis, would be necessary to get insight into the adaptive value of colour polymorphism in raptors and the reason for its spread, maintenance, consequences in fitness and breeding output (Chakarov *et al.* 2011), and first-year survival (Roulin *et al.* 2010).

Acknowledgements. We would like to thank Andreas Lindén, Alexandre Roulin and an anonymous referee for their valuable suggestions. We thank Ramón Ruiz, Iluminada Pagán, Mario León, Ginés Gómez and Carlos González for field assistance in the study area. This work was funded by the Spanish Ministerio de Educación y Ciencia (project REN2002-324 01884/GLO, partially financed by FEDER funds) and the Consejería de Agua, Agricultura y Medio Ambiente of the Region of Murcia. M. V. Jiménez-Franco was supported by a FPU grant from the Spanish Ministerio de Educación y Ciencia (reference AP2009-2073). P. López-López was supported by a “Juan de la Cierva-incorporación” postdoctoral grant of the Spanish Ministry of Economy and Competitiveness (reference JCI-2014-19190). Authorization for the study was provided by the Consejería de Agua, Agricultura y Medio Ambiente of the Region of Murcia.

Värimuoto ei vaikuta pikkukotkan pesyekokoon

Lintujen väripolymorfia saattaa vaikuttaa populaatioiden demografiaan ja siten myös kantojen vaihteluihin. Tässä artikkelissa tutkimme ensimmäistä kertaa värimuodon ja poikastuoton mahdollista yhteyttä pikkukotkalla, tarkastelemalla tilannetta Espanjan kaakkoisosissa sijaitsevassa populaatiossa. Käytimme aineistoa 19 vuoden jaksolta ei-merkityillä yksilöillä. Kokonaisuudessaan tarkastelun kohteena oli 738 vaaleata (91,6 %) ja 68 tummaa (8,4 %) aikuista pikkukotkaa 57 reviiirillä.

Tuloksemme mukaan värimuotojen osuudet populaatiossa pysyvät molemmilla sukupuolilla vakaina tutkimusjakson läpi. Vaikka tumman muodon vanhemmilla oli jokseenkin suurempi poikasmäärä vaaleaan muotoon verrattuna, ero ei ollut tilastollisesti merkitsevä. Siten, väripolymor-

fismi ei näytä oleva tärkeä selittäjä pikkukotkan lisääntymismenestykselle. Tosin, lisätutkimukset merkintä-takaisinpyyntianalysin muodossa ovat tarpeen, jotta voisimme ymmärtää miten värimuoto vaikuttaa yksilöiden kelpoisuuteen ja demografiaan populaatiotasolla tällä pitkäikäisellä lajilla.

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